Scotland's Rural College

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ASSESSMENT OF INFERTILITY IN WINTER WHEAT VARIETIES IN 1997/98 RECOMMENDED LIST AND NATIONAL LIST TRIALS

by

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Contents

Abstract

The relationship between ear fertility and yield was examined across winter wheat varieties grown in National List (NL) and Recommended List (RL) trials in Scotland, 1997. Fertility was defined as the percentage of florets to set seed. The number of grains and sterile grain sites per ear were recorded in 17 NL2/RL varieties at Aberdeen and Kelso and in 19 NL1 varieties at Aberdeen. Mean fertilities in NL2/RL varieties at Aberdeen and Kelso were 59% and 67%, respectively. Mean fertility in NL1 varieties was 50%. Yields of NL2/RL varieties at Aberdeen were 1.1-4.6 t/ha below the yield of their Kelso counterparts. Most of the selected NL1 and NL2/RL varieties at Aberdeen yielded significantly below their UK averages. Yields of NL2/RL varieties at Kelso were comparable to their UK averages. There were significant, linear, relationships between percentage ear fertility and yield across varieties. For every pertcentage reduction in fertility across NL2/RL varieties (at Aberdeen and Kelso) yield decreased by 75 kg/ha on average. In NL1 varieties yield decreased by 130 kg/ha for every percentage reduction in fertility. The level of fertility below which yield was significantly reduced was estimated to be between 62-69%. The proportion of sterile sites in the lower-middle part of the ear increased as percentage fertility decreased. These data strongly implicate fertility as an important factor in yield differences: (A) across varieties at the same location and (B) in some NL2/RL varieties between Aberdeen and Kelso. The data are discussed in relation to current knowledge of the physiological and environmental factors that influence fertility in wheat. The implications of this work include modification of breeding programmes as breeders discard material that might expose them and growers to vulnerable varieties. The main benefit for the industry is avoiding what could be very costly decisions for growers and breeders.

Introduction

Formation of grain is dependent on fertilisation of the ovum by pollen. Fertility affects the number of grains which develop in the ear. A reduction in fertility will suppress grain yield and affect grain quality. Furthermore, low levels of fertility encourage outcrossing with foreign pollen with consequences for the genetic purity of seed crops.

In recent years a number varieties of winter cereal species have exhibited reduced fertility. Ten years ago the winter wheat variety Moulin showed very low levels of seed set as a result of incomplete fertilisation. Losses to growers reached 90% in extreme cases. Although rare, another such occurrence cannot be ruled out, particularly as Moulin is regularly used as a parent in breeding programmes and has given rise to several candidate varieties. In addition to these extreme events, there is evidence that low levels of infertility that can affect yield remain undetected. The economic impact of undetected levels of infertility is not known, but another extreme case of reduced fertility would have serious consequences for growers and the UK cereal trade. The major proportion of the UK wheat area is dominated by only a few varieties which makes the cereal sector vulnerable should the fertility of a single variety fail.

SAC conducts National List variety trials in Scotland and is responsible for co-ordinating HGCA's Recommended List cereal variety testing in Scotland. A plant breeder expressed concern about levels of reduced fertility in a wheat trial in East Lothian in 1996 and at Kelso and Aberdeen in 1997: as a result of their comments SAC collected ear samples 1997.
Yield results from the Aberdeen trial showed a variety range from 1.7-9.5 t/ha. The Kelso yield range was 6.8-10.1 t/ha, whilst in East Lothian in 1996 the yield range was 10.1-12.3 t/ha. While infertility was strongly implicated as the cause of low yields at the Aberdeen site (both treated and untreated trials), the low yields at Kelso would have been recorded but not adequately explained. Thus the impact of infertility at the Kelso site would normally go unnoticed. In addition to the yield losses incurred at the 1997 Aberdeen trial site, there is evidence that undetected levels of infertility are depressing yields of wheat in Scotland. It is apparent that varieties are differentially affected, but we do not know if the same varieties are vulnerable at different sites and in different years.

The precise causes of reduced fertility are not known. Genotype susceptibility to sterility may be triggered by weather conditions, such as extremes of temperature, at critical stages of crop developments. The main objective of our study was to assess fertility in the samples collected from the Aberdeen and Kelso trial sites and to establish if there was a relationship between fertility and yield across varieties. Other objectives were: to identify genotypes at risk, assess the risk that cross-pollination occurred resulting in hybrid seed and to discuss fertility in relation to developmental events as influenced by environmental factors.

Materials and Methods

Sites and plant material

Plant material was collected from plots in National List 1 (NL1) and National List 2 /Recommended List (NL2/RL) variety trials at Tillycorthie Farm, near Aberdeen and from the NL2/RL variety trial at Spotsmains Farm, near Kelso in the Scottish Borders. Site and agronomic details are shown in Table 1. Three weeks before harvest 1997 approximately twenty ears were collected from each variety in a fungicide-treated block of the NL1 and NL2/RL trials. The samples were stored in a laboratory until measurement of fertility.

Table 1. Details of trial locations and agronomic practices

Site	Tillycorthie, Aberdeen	Kelso, Borders
Trial	NL1 and NL2/RL	NL2/RL
National Grid Ref.	NJ 909 233	NT 660 362
Altitude (m)	100	150
Meteorological station	Craibstone (near Aberdeen)	Bush Estate (near Penicuik)
Soil type	Sandy loam	Sandy loam
Previous crop	Spring oilseed rape	Winter oilseed rape
Sowing date	10 October 1996	8 October 1996
Nitrogen applications (kg/ha, date and GS)	50, 6.3.97, GS21-22 130, 18.4.97, GS30-31	13, 4.10.96, GS05 70, 11.3.97, GS15-22 110, 11.4.97, GS25-30
Herbicide applications (dates and GS)	9.4.97, GS30 17.4.97, GS30-31	5.11.96, GS12 18.4.97, GS30-31
Fungicide applications (dates and GS	30.4.97, GS 32 16.5.97, GS37-39 8.7.97, GS60	30.4.97, GS31-32 27.5.97, GS37-39 17.6.97, GS60-65
Growth regulators (date and GS)	9.4.97, GS30	18.4.97, GS30-31

Mean and minimum daily air temperatures are shown for the period between mid May to late July (Figure 1): this corresponds to the growth stages (GS) between flag leaf emergence and anthesis. At Aberdeen there were three consecutive days at approximately booting stage when the minimum temperature was between 0.7-2.1°C and two days at approximately ear

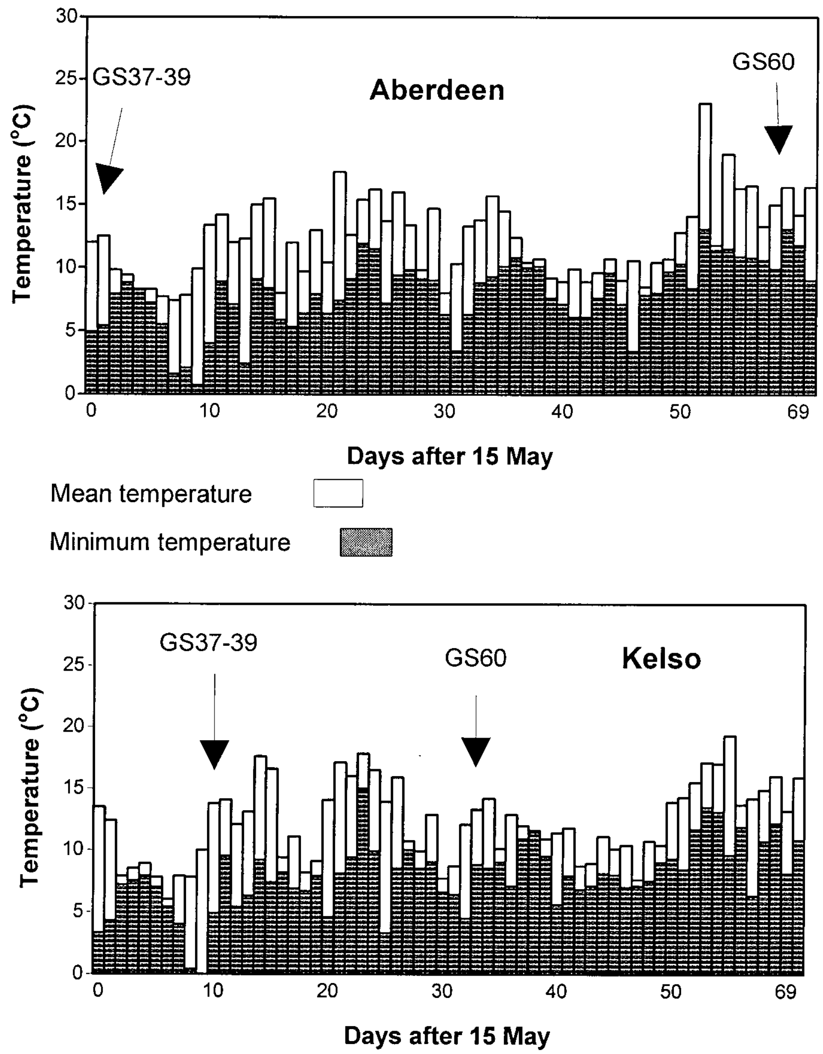

Figure 1. Mean and minimum daily air temperatures for the period between mid May to late July at Craibstone meteorological station (reference for the Aberdeen trial site) and the Bush Estate (estimate for the Kelso trial site).

emergence when the minimum temperature was 3.4 °C. In the Borders area there were two consecutive days at approximately flag leaf appearance when the minimum temperature was less than 1°C and three days between flag leaf emergence and anthesis when the minimum temperature was below 5 °C.

Assessments of fertility

Fertility was measured in 17 varieties from the two NL2/RL trials (the same varieties in both trials) and in 19 varieties from the NL1 trial. Varieties were selected to provide a representative range of yields at the two sites. Ears were dissected and assessed for fertility according to a procedure developed by Nickerson UK Ltd. Eight ears were laid flat on a bench with a row of spikelets facing upwards. Starting with the spikelet at the base of the ear, the glumes of each floret where opened using a pair of forceps and the floret was recorded as either grain present or a sterile site. Using a specially-designed recording sheet the position of each grain was numbered and sterile sites were shaded red. All grains were removed from the ear and stored in individual slots of a micro titre-tray. This procedure was completed for both sides of the ear. Percentage fertility was expressed as

$$\frac{s}{s+f}x100$$

where s = number of sterile sites
and f = number of fertile sites

An example of an assessment of a single ear is shown in Figure 2.

A sterile floret was defined as one with no grain at maturity, but which contained the remains of floral parts (e.g. carpel and anthers). To reduce the likelihood of counting late developing florets only those florets with lemmas at least 3 mm long were recorded. The definition of sterility was adapted from Rawson and Bagga (1979) and Rawson (1995). Florets in which grain had formed but was missing were recorded as grain absent (this occurrence was rare).

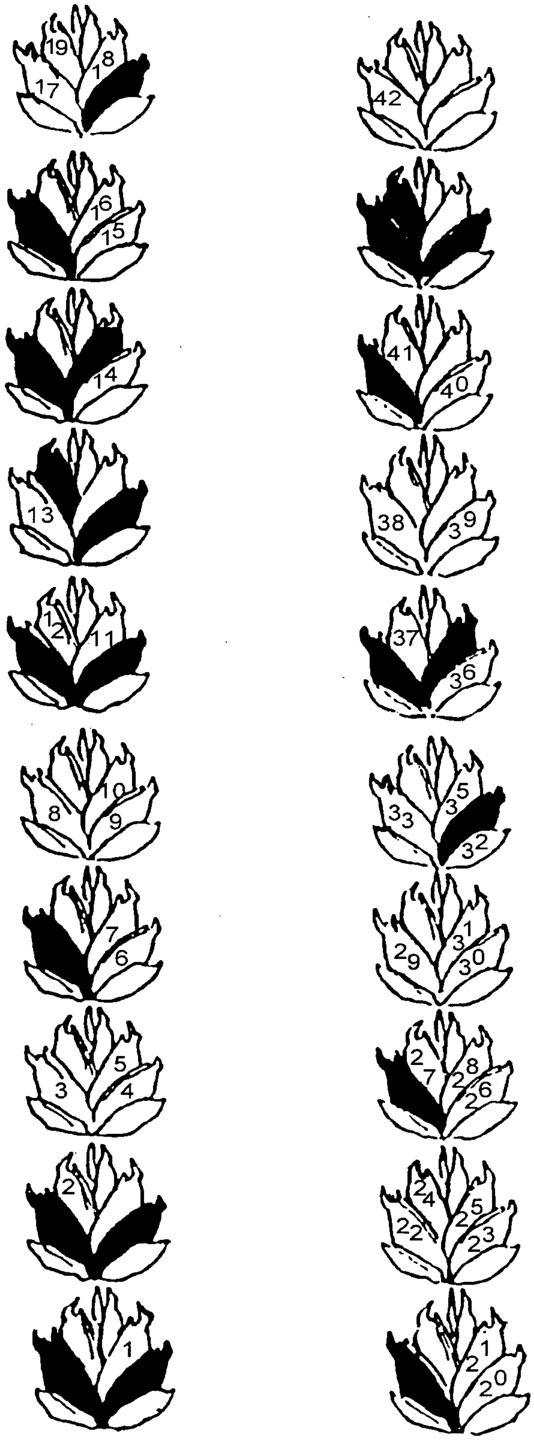

Figure 2. Assessment of ear fertility. This example shows how each spikelet on both sides of the ear were scored for grain present (numbers) and sterile site (shaded area). There were 42 grains and 22 sterile sites giving a % fertility of 42/(42+22) x 100 = 66%.

The distribution of sterility within ears was determined by counting the number of sterile sites in the base, lower middle, upper middle and tip regions (quarters) of the ear. These counts were also expressed as proportions of sterile sites for the ear as a whole

Other calculations

Grain yields were determined from replicated fungicide-treated plots adjusted to t/ha at 15% moisture content. Yield was expressed in two other ways. Firstly, yield was calculated as a % of the mean yield of Brigadier, Hereward, Hunter, Hussar and Riband (control varieties). Secondly, % yield was divided by the % yield for all UK sites. This ratio enables yield data to be compared on a relative scale where 1 = expected yield relative to the UK as a whole. That is, the ratio removes inherent differences between varieties and sites.

Electrophoresis

The ears of two NL2/RL varieties from Aberdeen were examined for genetic purity using SDS electrophoresis. Forty-eight grains were removed (from two ears) of the varieties Brigadier and Pentium. The grain was then cut in half and the endosperm milled using a small electric drill. The milled endosperm was used for electrophoresis and the embryo was retained for growing on if required. The electrophoresis was standard SDS page.

Results

The mean yield of NL2/RL varieties at Aberdeen (6.2 t/ha) was significantly below the UK mean of 8.6 t/ha (Table 2). By contrast, the mean yield for NL2/RL varieties at Kelso was not significantly different from the UK mean. The yields of NL2/RL varieties ranged between 3.6-9.5 t/ha at Aberdeen and 6.8-10.1 t/ha at Kelso, this compared with a UK range of 7.3-9.4 t/ha. The mean yield of NL1 varieties at Aberdeen (6.0 t/ha) was significantly below the UK mean of 8.0 t/ha (Table 3). The yields of NL1 varieties ranged between 1.7-9.5 t/ha, compared with a UK range of 6.9-9.4 t/ha.

In 1997, the mean yields of control varieties (Brigadier, Hussar, Rialto, Riband and Hereward) were 7.78 t/ha and 9.25 t/ha at Aberdeen and Kelso, respectively, compared to 8.94t/ha for the UK (Table 4A). Table 4B shows the The average yield of control varieties at Aberdeen and Kelso/Berwickshire (Borders) between 1992-1997. With the exception of 1994 the control yields were higher in the Borders than at Aberdeen

Nine out of 17 NL2/RL varieties at Aberdeen were >20% below their UK values (Table 2). There was less variation in percentage (%) yields at Kelso than at Aberdeen. With one exception % yields of NL2/RL varieties at Kelso were within ±7% of their UK values (Table 2). Eleven out of 19 NL1 varieties at Aberdeen were >20% below their UK values; of this group four were >40% below their UK values (Table 3).

The mean ear fertility for NL2/RL varieties at Aberdeen was 59% (range 31-87%) compared to 67% at Kelso (range 42-81%) (Table 2). At Aberdeen, 9 NL2/RL varieties had fertility levels <60%, whereas at Kelso 4 varieties were <60% fertility. NL1 varieties at Aberdeen had a mean ear fertility of 50%, with a range of 12-71%. Twelve NL1 varieties had fertility levels <60%; of this group, 5 varieties had fertility levels <40% (Table 3).

There were significant linear relationships between percentage ear fertility and yield (Fig. 3). For NL2/RL varieties there was no significant difference in the direction of the slopes between locations (Fig. 3A and B) and a single slope, with separate constants for each location, was fitted, as shown in Fig. 4. The average slope of the line for predicted yield of varieties was 0.075. That is, for every % increase in fertility across varieties the yields increased by 75 kg/ha on average. The slope of the line for predicted yield against % fertility

Table 2. Yield and fertility of NL2/RL varieties at Aberdeen and Kelso, compared with yield for UK

	Aberdeen			Kelso			UK	
Variety	Yield (t/ha)	Yield (%)	Fertility (%)	Yield (t/ha)	Yield (%)	Fertility (%)	Yield (t/ha)	Yield (%)
Riband	7.4	95	87	9.4	102	78	9.0	100
Brigadier	8.3	107	82	9.5	103	81	9.0	100
Savannah	8.6	110	77	10.1	109	77	9.3	104
Madrigal	9.5	123	76	10.1	109	73	9.4	105
Caxton	5.9	75	74	8.9	96	76	8.6	97
Maverick	6.1	79	69	8.7	95	70	9.0	101
Oberon	5.7	73	68	8.5	92	67	8.8	99
CWW 95/23	6.3	81	63	9.3	101	69	8.7	97
Spark	7.5	96	58	8.5	91	57	8.3	92
CWW 95/41	8.6	111	55	9.7	104	77	9.3	104
CWW 95/57	5.8	75	53	8.8	95	66	8.1	91
Krakatoa	4.8	61	50	8.9	96	60	8.7	98
Cebeco 954	4.7	60	49	8.1	88	75	7.3	82
NSL WW12	3.6	46	38	6.8	73	57	8.0	89
Equinox	4.3	56	37	8.9	96	53	9.0	101
CPBT W43	4.8	62	37	8.5	91	61	8.7	97
Pentium	3.7	47	31	7.3	79	42	7.5	84
Mean	6.2	80	59	8.8	95	67	8.6	97
s.e.	0.44	5.7	4.2	0.21	2.3	2.6	0.15	1.6

Table 3. Yield and fertility of NL1 varieties at Aberdeen compared with yield for UK

	Aberdeen			UK	
Variety	Yield (t/ha)	Yield (%)	Fertility (%)	Yield (t/ha)	Yield (%)
CPBT W47	9.5	118	71	9.3	106
HYB 95-125	9.1	113	69	9.1	104
Flair	9.1	113	67	8.6	98
CWW 96/17	9.1	114	64	9.4	108
Z496	8.1	101	64	9.3	106
NSL WW15	8.0	100	63	8.8	100
CPBT W40	7.0	88	60	8.8	101
FD 94 037	4.7	58	56	6.9	79
Z696	4.7	58	52	7.9	91
Z596	8.8	110	51	9.2	105
NSL WW16	5.4	68	51	8.6	99
CWW 96/119	3.3	41	51	7.9	90
Z796	5.1	63	49	7.8	89
94.10	4.9	61	45	8.0	92
CPBT W50	4.7	59	39	8.1	92
CWW 96/39	4.5	56	35	7.8	89
CWW 96/21	4.2	53	34	8.3	95
94.11	1.7	21	15	7.3	84
94.08	2.0	25	12	7.4	84
Mean	6.0	75	50	8.0	95
s.e.	0.6	7.6	4.1	0.2	2.1

Table 4A. Mean yield of control varieties (Brigadier, Hussar, Rialto, Riband and Hereward) at Aberdeen and Kelso compared to the UK as a whole in 1997.

	Aberdeen	Kelso	UK
Yield	7.78	9.25	8.94
s.e.	0.38	0.23	0.16

Table 4B. Mean yield of control varieties (Brigadier, Hussar, Rialto, Riband and Hereward) at the Aberdeen and the Borders sites between 1992-1997.

	Aberdeen	Borders
1992	10.29	11.80^{B}
1994	10.43	7.53^{B}
1995	9.12	10.89^{B}
1996	8.46	11.29^{K}
1997	7.78	9.25^{K}
Mean	9.22	10.15

Notes: There was no yield data from Aberdeen in 1993.
^{B}Berwickshire site; ^{K}Kelso site

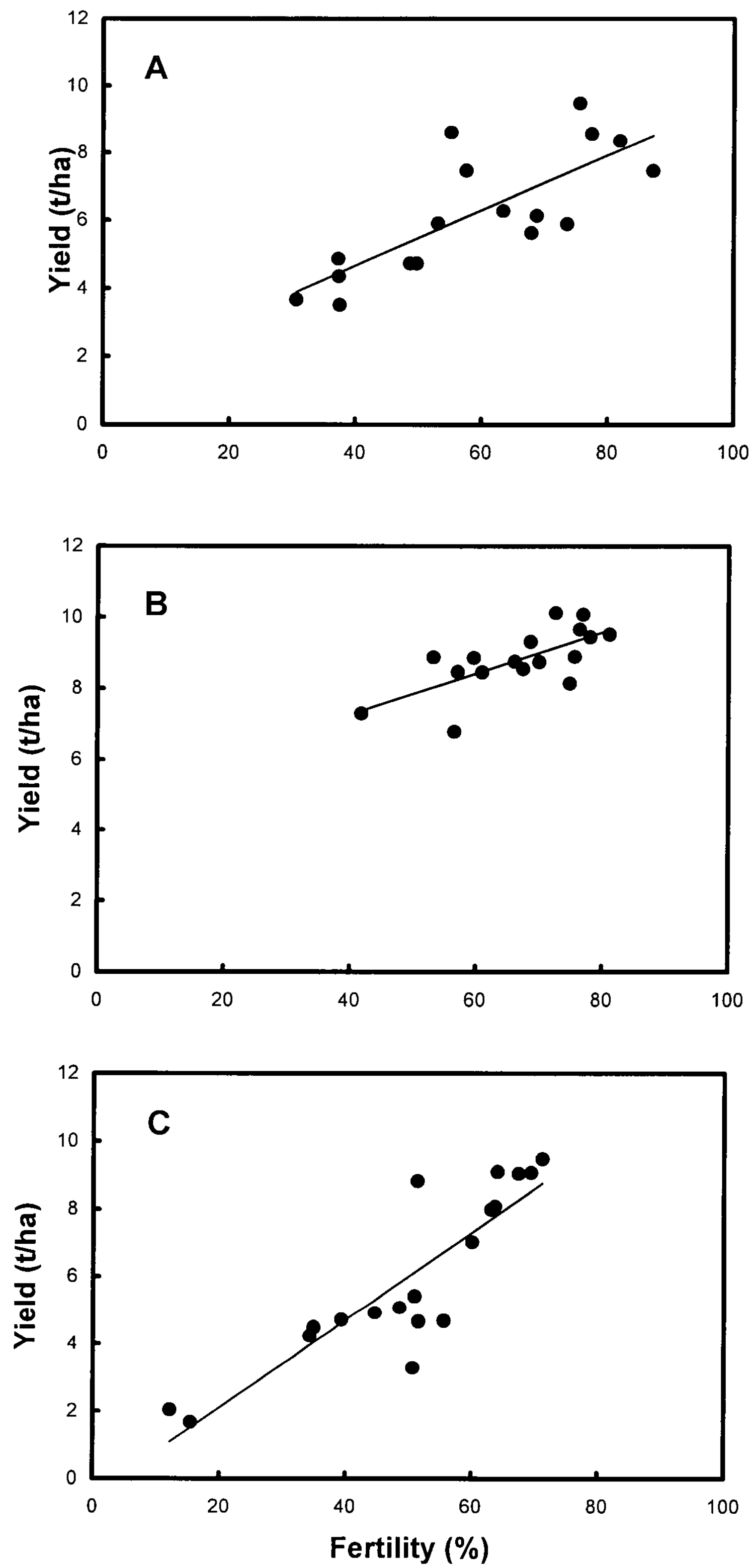

Fig. 3. Relationship between ear fertility (%) and yield (t/ha) in (A) NL2/RL varieties at Aberdeen, slope of regression = 0.081, r^2 = 0.59; (B) NL2/RL varieties at Kelso, slope of regression = 0.058, r^2 = 0.76; (C) NL1 varieties at Aberdeen, slope of regression = 0.13, r^2 = 0.76. Each data point represents the one variety.

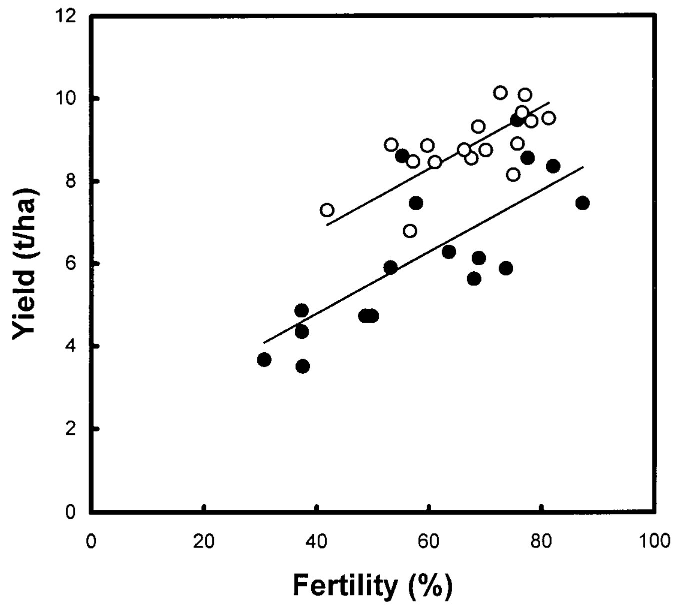

Fig. 4. Relationship between ear fertility (%) and yield (t/ha) in NL2/RL varieties at Aberdeen (●) and Kelso (○). Slope of regressions = 0.075.

of NL1 varieties at Aberdeen was 0.13 (Fig. 3C). That is, an increase of 130 kg/ha per % increase in fertility.

Ratios of % yield to % UK yield are shown in Fig. 5. Each data point represents a variety's performance relative to its expected yield (i.e. yield = 1.0). The upper confidence interval indicates the level of fertility at which the predicted yield of varieties falls significantly below the expected yield: this was 69% for NL2/RL varieties at Aberdeen (Fig. 5A), 63% for NL2/RL varieties at Kelso (Fig. 5B) and 62% for NL1 varieties at Aberdeen (Fig. 5C).

Further analyses of ears are shown in Tables 5-7. NL2/RL varieties at Kelso and NL1 varieties at Aberdeen had on average 2 more spikelets per ear than NL2/RL varieties at Aberdeen (Tables 5A, 6A and 7A). Within each trial the number of spikelets per ear varied little between varieties. With the exception of Riband and Savannah, each NL2/RL variety had fewer grains per ear at Aberdeen than at Kelso (Tables 5A and 6A). The mean number of grains per ear for NL2/RL varieties at Aberdeen was 37, this was significantly less than the mean number of 50 grains per ear at Kelso. At both NL2/RL locations, the mean number of sterile grain sites per ear was 25. For NL1 varieties at Aberdeen, both mean grain number per ear and mean number of sterile grain sites per ear was 37 (Table 7A).

The number of grains per spikelet was greatest in NL2/RL varieties at Kelso and least in NL1 varieties at Aberdeen (Tables 5A and 7A). In each trial, the best yielding (or most fertile) varieties had at least 2.5 grains per spikelet. With one exception each NL2/RL variety at Kelso had 2 or more grains per spikelet. By contrast, several NL2/RL and NL1 varieties at Aberdeen had fewer than 2 grains per spikelet.

Generally, the higher yielding (or more fertile) NL2/RL varieties had fewer sterile grain sites per ear at Aberdeen than their counterparts at Kelso. By contrast, the lower yielding (or less fertile) NL2/RL varieties tended to have more sterile sites per at Aberdeen than their counterparts at Kelso (Tables 5A and 6A).

The distribution of sterile grain sites within the ear was influenced by the level of fertility (Fig. 6). For most varieties, in each trial, the mean number of sterile sites was least just below the mid point of the ear (lower-middle) and highest at the tip of the ear (Tables 5B, 6B and 7B). On average the proportions of sterile sites in the basal, lower middle, upper middle and

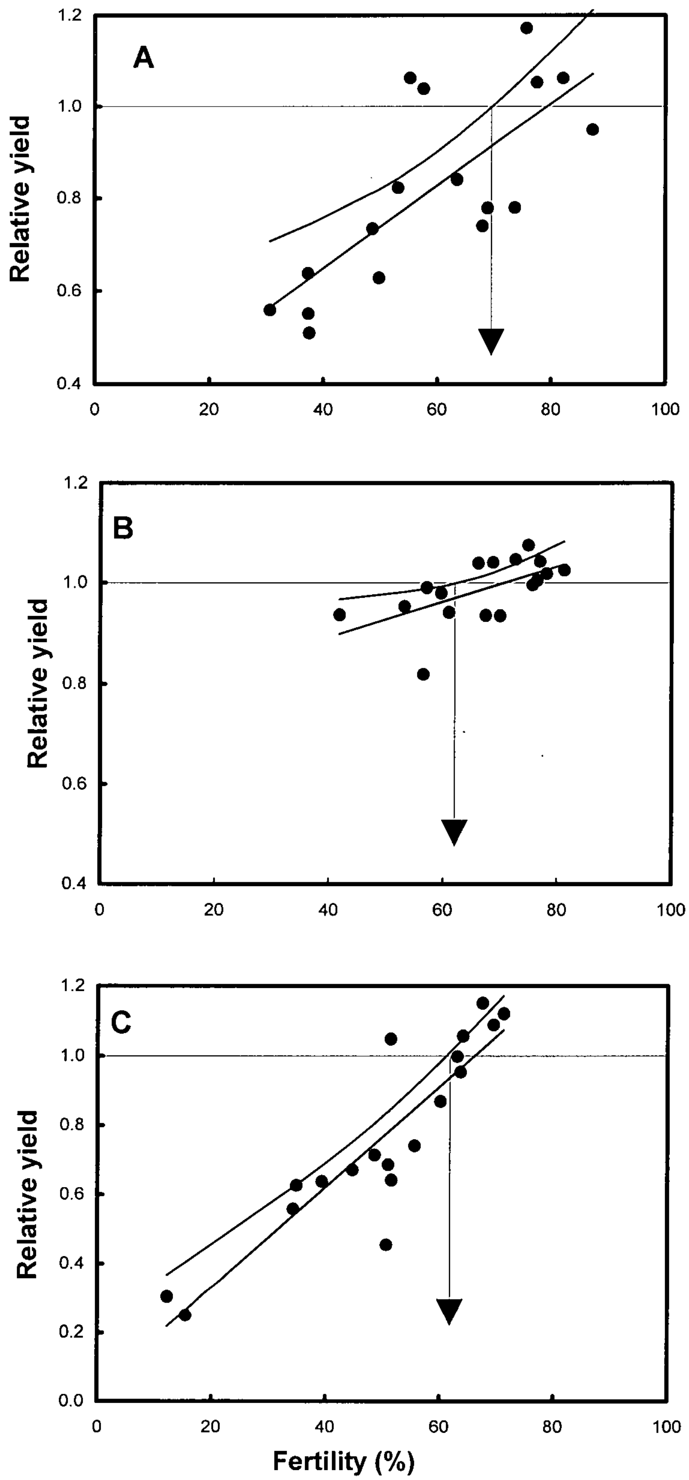

Fig. 5. Relationship between ear fertility (%) and relative yield (% yield is expressed as a proportion of % UK yield) in (A) NL2/RL varieties at Aberdeen, (B) NL2/RL varieties at Kelso and (C) NL1 varieties at Aberdeen. Each plot shows the linear regression with its upper 95% confidence interval (CI). The point at which the CI intercepts yield = 1.0 indicates the fertility below which the predicted yield for varieties falls below the expected yield, as shown by the arrow.

Table 5. (A) Counts of grains and sterile sites per ear and (B) Distribution of sterile grains within ears of NL2/RL varieties at Aberdeen

(A)					(B)			
					Distribution of sterile sites in ear			
Variety	Spikelets per ear	Grains per ear	Grains per spikelet	Sterile sites per ear	Base	Lower-mid	Upper-mid	Tip
Riband	19	63	3.3	9	2	1	2	4
Brigadier	17	41	2.5	9	2	2	2	3
Savannah	19	55	3.0	16	4	2	3	8
Madrigal	18	53	2.9	17	6	2	3	6
Caxton	18	44	2.4	15	4	4	4	4
Maverick	18	40	2.2	17	4	3	3	6
Oberon	17	35	2.0	16	4	3	5	4
CWW 95/23	18	37	2.0	21	5	4	7	5
Spark	17	38	2.2	27	7	4	7	9
CWW 95/41	19	40	2.1	32	8	5	9	10
CWW 95/57	16	34	2.1	28	6	6	8	8
Krakatoa	18	30	1.6	30	7	5	9	10
Cebeco 954	20	37	1.9	39	11	7	10	12
NSL WW12	19	26	1.4	43	12	10	10	11
Equinox	19	22	1.2	36	9	7	10	9
CPBT W43	18	26	1.4	44	10	9	13	12
Pentium	18	15	0.9	33	8	7	9	9
Mean	18	37	2.1	25	6.4	4.7	6.6	7.6
s.e.	0.24	2.95	0.16	2.76	0.72	0.65	0.81	0.71

Table 6. (A) Counts of grains and sterile sites per ear and (B) Distribution of sterile grains within ears of NL2/RL varieties at Kelso

(A)					(B)			
					Number of sterile sites within ear			
Variety	Spikelets per grain	Grains per ear	Grains per spikelet	Sterile sites per ear	Base	Lower-mid	Upper-mid	Tip
Riband	20	57	2.9	16	4	2	4	6
Brigadier	19	60	3.1	14	3	2	3	6
Savannah	19	54	2.9	16	4	2	3	7
Madrigal	20	54	2.8	20	6	4	3	7
Caxton	20	56	2.8	19	4	2	5	8
Maverick	20	53	2.6	24	6	5	6	9
Oberon	21	53	2.6	26	8	4	6	8
CWW 95/23	20	53	2.6	25	7	4	6	8
Spark	21	45	2.2	35	9	6	9	11
CWW 95/41	20	59	2.9	19	4	2	4	9
CWW 95/57	18	44	2.5	22	6	3	6	8
Krakatoa	17	39	2.2	26	5	4	6	10
Cebeco 954	24	69	2.9	23	4	3	6	11
NSL WW12	19	40	2.1	30	9	5	8	9
Equinox	20	40	2.0	35	8	6	9	12
CPBT W43	21	46	2.2	29	7	5	7	10
Pentium	20	33	1.7	43	9	8	12	14
Mean	20	50	2.5	25	6.0	3.9	5.9	8.9
s.e.	0.35	2.25	0.09	1.89	0.49	0.44	0.59	0.52

Table 7. (A) Counts of spikelets, grains and sterile sites per ear and (B) Distribution of sterile grains within ears of NL1 varieties at Aberdeen

(A)					(B)			
					Distribution of sterile sites in ear			
Variety	Spikelets per ear	Grains per ear	Grains per spikelet	Sterile sites per ear	Base	Lower-mid	Upper-mid	Tip
CPBT W47	20	58	2.7	24	5	3	7	10
HYB 95-125	20	54	2.7	24	5	3	6	10
Flair	21	56	2.7	26	5	4	6	11
CWW 96/17	20	48	2.4	26	7	4	7	9
Z496	17	32	1.9	18	5	3	4	6
NSL WW15	19	47	2.5	27	6	4	7	10
CPBT W40	19	43	2.3	29	7	6	7	10
FD 94 037	22	44	2.1	37	8	7	11	12
Z696	20	39	2.0	36	8	6	11	12
Z596	17	33	1.9	31	7	8	8	9
NSL WW16	19	36	1.9	34	9	7	8	11
CWW 96/119	20	39	2.0	36	9	7	9	11
Z796	21	39	1.8	42	10	8	12	12
94.10	20	34	1.7	40	10	10	10	11
CPBT W50	18	25	1.4	42	12	10	10	10
CWW 96/39	18	24	1.3	42	11	10	10	12
CWW 96/21	21	26	1.3	53	14	11	15	14
94.11	20	12	0.6	64	17	16	16	15
94.08	19	9	0.5	65	18	16	16	15
Mean	20	37	1.9	37	8.9	7.4	9.3	11.0
s.e.	0.30	3.09	0.14	2.95	0.89	0.91	0.77	0.49

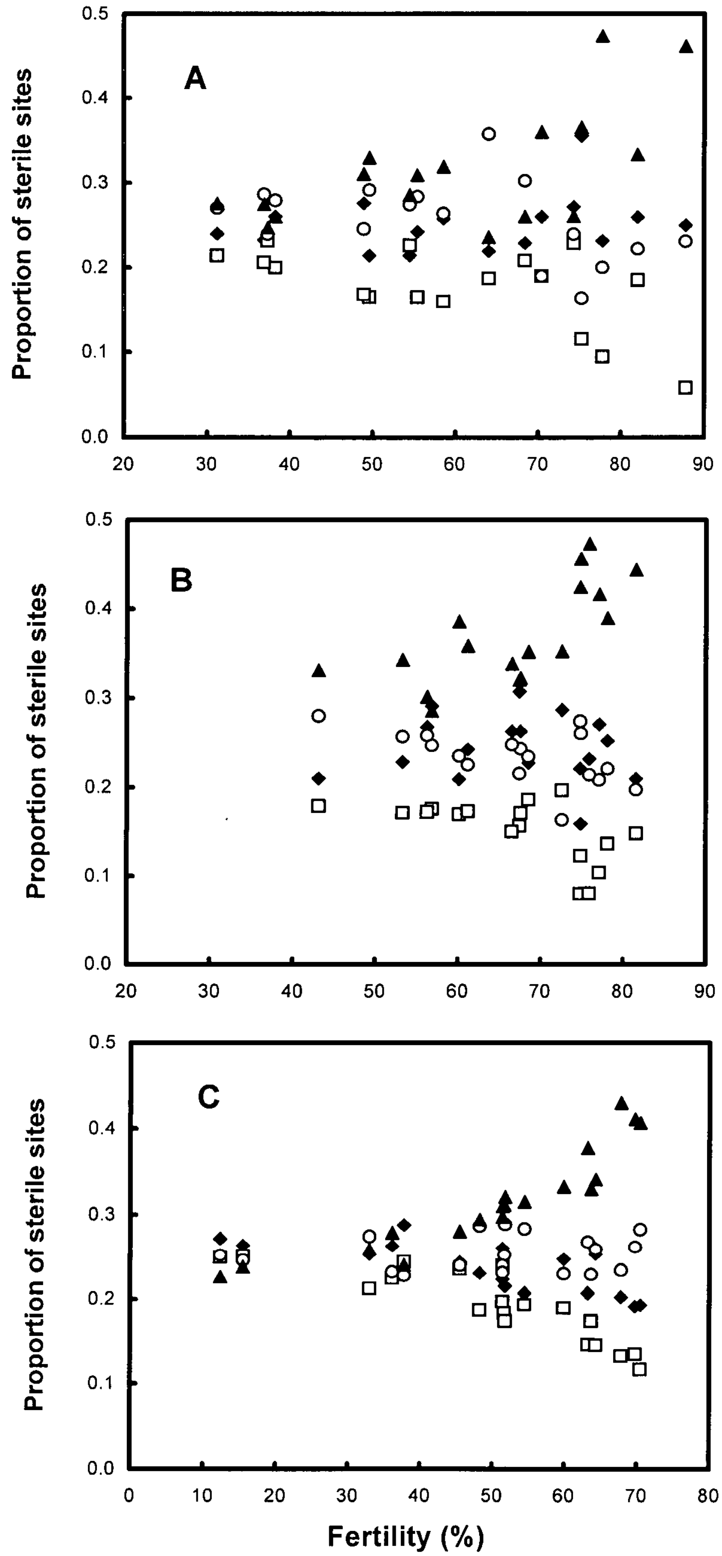

Fig. 6. Relationship between fertility (%) and the proportions of sterile grain sites in the base (◆), lower-middle (□), upper-middle (O) and tip (▲) of (A) NL2/RL varieties at Aberdeen, (B) NL2/RL varieties at Kelso and (C) NL1 varieties at Aberdeen.

tip regions of the ear were approximately 0.25, 0.17, 0.25 and 0.33. However, when fertility was very low (<40-50%) the number of sterile sites in each section of the ear were approximately equal (Fig. 6 A-C). As fertility increased the proportion of sterile sites at the tip increased, but the proportion of sterile sites in the lower-middle part of the ear decreased. (Fig. 6A-C).

The ears of two NL2/RL varieties from Aberdeen were examined for genetic purity using electrophoresis. Forty-eight grains were examined (from two ears) of the varieties Brigadier and Pentium. Brigadier has the high molecular weight glutenin pattern null 6+8, 2+12. No offtypes were recorded. Pentium has the subunit composition 1, 7, 2+12. Thirty-three grains were found to be of this type whereas, 15 grains were found to be hybrid grain with the dominant hybrid 1,7/6+8, 2+12. The hybrids were clearly identified as they had the combination of both parental types. Tables 8 and 9 indicate the parentage of NL2/RL and NL1 varieties, respectively. Several lines are common to varieties with low fertilities: in particular Moulin, Rendezvous and Talon.

Table 8. Parentage of NL2/RL varieties

Variety	Parents
Riband	Norman x (Maris Huntsman x TW161)
Brigadier	Squadron x Rendezvous
Savannah	Riband x Brigadier
Madrigal	Hussar x Beaver
Caxton	Moulin x Riband
Maverick	Talon x Torfrida
Oberon	(Beaver x Torfrida) x Hussar
CWW 95/23	Talon x Torfrida
Spark	Moulin x Tonic
CWW 95/41	Hussar x (Haven x complex experimental cross)
CWW 95/57	(Fresco sib x Moulin x VPM41.22.11)) x Rendezvous x Torfrida
Krakatoa	Apollo x CWW442/64
Cebeco 954	Moulin x Pontiac
NSL WW12	Composite cross
Equinox	CWW 442/64 X (Rendezvous x Obelisk)
CPBT W43	(Cadenza x Lynx sib) x Lynx
Pentium	Talon x Rendezvous

Table 9. Parentage of NL1 varieties

Variety	Parents
CPBT W47	Rialto x 24-1-420
HYB 95-125	Hyb93-16 x Piko
Flair	Ares x Marabu
CWW 96/17	Hussar x Lynx
Z496	4215-4-2 x Hussar
NSL WW15	Composite cross
CPBT W40	(Talon x Beaver) x Lynx sib
FD 94 037	FS81033 x Hereward
Z696	4215-5-1 x Hunter
Z596	4215-5-1 x Brigadier
NSL WW16	Composite cross
CWW 96/119	(Haven x Torfrida) x Torfrida)
Z796	4215-4-2 x Hussar
94.10	Moulin x Drakkar x Marathon
CPBT W50	(Cadenza x 24-1-420) x Lynx
CWW 96/39	((Fresco sib (Moulin x VPM41.22.11)) x Rendezvous) x Torfrida
CWW 96/21	Rialto x Morell
94.11	Moulin x Drakkar x Marathon
94.08	Moulin x Arminda

Discussion

Results in this study indicate that some varieties are more susceptible to floret sterility than others and that there is a strong relationship between % fertility and yield across varieties grown at the same location. Some varieties compensate better than others for a loss of grain number as a result of floret sterility and this will contribute to variability about the % fertility *x* yield relationship. In general, for every % decrease in fertility in NL2/RL varieties there was a decrease in yield of 75 kg/ha on average. This relationship was consistent for both the 'high' yielding location at Kelso (where most NL2/RL varieties yielded better than their UK average) and the 'low' yielding location at Aberdeen (where most varieties yielded significantly below their UK average). In NL1 varieties the decrease in yield with a reduction in fertility was more pronounced with a loss of 130 kg/ha for every % decrease in fertility.

A location (or climatic) effect on yield of NL2/RL varieties can be estimated from the difference in intercepts of the slopes for Aberdeen and Kelso in Fig. 4; this was approximately 2 t/ha. Thus, the difference yield between the two locations was large compared to the differences in fertility. Although it is unlikely that fertility *per se* explains the differences in yield between all varieties, it is apparent that fertility strongly influences the yield of some individual varieties between sites, especially those with low fertility scores. For example, if Aberdeen NL2/RL varieties with fertilities above 50% are compared with their counterparts in Kelso, then the difference in mean fertility is only 2%. By contrast, if Aberdeen NL2/RL varieties with fertility scores of 50% or less are compared with their Kelso counterparts then the difference in their mean yield is 3.8 t/ha with a difference in fertility of 18%.

The plots in Fig. 5 indicate the yields of varieties relative to their performance nationally. On this scale the absolute difference in yield Aberdeen and Kelso is removed, as are inherent differences between high yielding and low yielding varieties. All but one of the Kelso NL2/RL varieties yielded more than 90% of its 'expected' value; and most varieties yielded close to their UK % yield. Hence the shallow slope. With a few exceptions (e.g. Brigadier, Savannah and Madrigal) most of the Aberdeen NL2/RL varieties yielded less than 80% of their expected value.

Table 10 indicates how our results can be used to define degrees of fertility. It is unlikely that fertilities above 85% will result in a significant yield loss. An average or 'normal' level of fertility is dependant on variety and location and could range between 65-90%. However, there is the possibility of a small yield reduction or even a significant yield loss at the lower end of this range. Although it is not known if low (sub-clinical) or undetected levels of sterility are suppressing yields in wheat nationally our results suggests that wheat ears have the capacity to compensate for fertility as low as 62-69% (Fig. 5). If fertility is less than 60-65% then yield loss is likely to be significant. Below 45-50% fertility yield is likely to be very poor. The varieties most at risk appear to be the NL1's and NL2/RL's scoring less than 40% fertility. Other varieties with fertility scores in the range 50-60% may be considered as having intermediate risk.

Table 10. Definitions of fertility and consequences for yield.

Fertility %	< 40	40	50	60	70	80	90	100
Definition of fertility	Very low		Low		Average (Normal)		High	
Effect on yield	Very poor yield		Significant yield reduction		None or small loss (undetected) or occasionally significant		No yield loss or undetected	

Analysis of two NL2/RL varieties (from Aberdeen) for genetic purity using electrophoresis indicated that in some cases the levels of infertility measured are likely to be an underestimate. In Brigadier, which had a relatively high fertility (78%), there were no offtypes found. By contrast, in Pentium, which had a fertility of only 31%, there was evidence of a significant number of hybrid offtypes. Thus, low levels of fertility encourages outcrossing with foreign pollen with consequences for the genetic purity of seed crops.

As well as floret sterility there are other aspects of development and survival of both spikelets and florets that determine grain number per ear: for example, not all spikelets and florets will survive to form grains. Although the better yielding NL2/RL varieties at Aberdeen had fewer sterile grain sites than their counterparts at Kelso, a lower grain number per ear may have contributed to their depressed yield. By contrast, the lower yielding NL2/RL varieties at Aberdeen had more sterile sites than their Kelso counterparts, this appears to have exacerbated the yield difference between the two sites. Our data suggest that varieties are particularly vulnerable to yield loss when sterility has resulted in less than 2 grains per spikelet on average. If spikelet number is low, then at least 2.5 grains per spikelet are required to avoid yield loss. It would be useful to establish if the differences in potential grain number (number of grains + number of sterile sites) between Aberdeen and Kelso were typical of those sites, irrespective of seasonal variation in % sterility.

The first spikelets to initiate florets are the larger ones just below the centre of the ear: these spikelets appear as double ridges first (Rawson, 1995). Spikelet development proceeds laterally and longitudinally until the basal and terminal spikelets appear (Bonnet, 1935; Rawson, 1995). It appears that when fertility is high the 'weaker' florets (later formed florets that are less competitive for resources) are the most likely to become sterile whilst the 'stronger' florets (first formed florets that are more competitive for resources) have greater chance of grain set. However, during circumstances that result in low fertility the 'stronger' florets are equally susceptible. Our suggests that a more equal spread of sterile sites in susceptible varieties could result in a loss of six or more grains from the lower-central part of the ear.

Although precise causes of infertility are not known, genotype susceptibility triggered by critical environmental conditions can be strongly implicated. The sequential nature of spikelet development may result in the more central spikelets forming florets before the terminal spikelet has appeared (Rawson, 1971). This pattern of development can result in asynchrony of anther development in different parts of the ear. Consequences of asynchrony may be that short periods of exposure to stresses such as low temperature or frosts damage a limited number of florets that are at a susceptible stage of their development. A lengthy period of stress may cause damage to the whole ear (Rawson, 1995).

It is possible that earlier developing genotypes, or early sowing, increases the risk of exposure to weather conditions that predispose a plant to reduced fertility. Low temperatures during flowering are known to affect fertility (Qain *et al.*, 1985; Skinnes and Burås, 1987). High sensitivity to frost damage between terminal spikelet and anthesis may result in partial or whole crop sterility (Single, 1971; Marcellos, 1977). Qian *et al.* (1986) suggest that varieties vary in their ability to develop normal anthers and pollen under low temperatures and showed that when day-night temperature was reduced (from $15^{o}/10^{o}C$ to $11^{o}/6^{o}C$) the duration of pollen development lengthened and flowering time was delayed and the percentage of spikelets setting seed was reduced. Doussinault *et al.* (1988) showed that pollen production in wheat decreased in cold springs, and there was a negative correlation between the percentage of abnormal pollen and the level of seed setting.

The influence of periods of low temperature at Aberdeen and Kelso on floret fertility are not clear because they coincided with several, critical, growth stages. However, our data, and results from elsewhere, suggests that further work on the effects of low temperature on floret development, under UK conditions, is a key area for further study.

It is less clear if high temperature alone affects sterility, but Rawson (1995) hypothesises that high temperature may accelerate development (e.g. spikelet development) and therefore reduce the time during which the plant can take up nutrients or accumulate photosynthates during critical development stages immediately before or after anthesis. Tashiro and Wardlaw (1990) demonstrated that high humidity increases sterility. This may be a result of reduced uptake of essential nutrients (e.g. boron) because of lower transpiration at high humidity as described by Rawson (1995a and b).

Carbon shortage as a consequence of reduced photosynthetic activity during periods of low temperature (Marcellos, 1977) and low irradiance during flowering (Batch and Morgan, 1974) has been implicated in low fertility. However, an alternative view is that low carbon supply alone is unlikely to result in sterility; rather, the uptake of nutrients could be a more important factor than carbon supply and deficiency in boron has been implicated in low fertility in wheats grown in South East Asia (Huang *et al.*, 1995; Rawson and Noppakoonwong, 1995). Unlike floret fertility, floret number is influenced by the availability of photoassimilates (Wardlaw, 1994). It is likely that stressful conditions resulting in low carbon availability will increase the number of grains that fail to complete growth, especially in distal florets near the tip of the ear (Rawson and Ruwali, 1972). Competition for assimilates after anthesis means that the basal florets, which are the most advanced, have an advantage over the upper florets; especially when the plant in under stress (e.g. drought or high tiller number). Thus the upper florets may not complete their development (Rawson, 1995).

A critical stage for loss of fertility is likely to be at meiosis, and it is at this stage that the floret appears particularly vulnerable to stress. Fertility can be reduced by interruption to meiosis in the anther and carpel (Bennett *et al.*, 1973). Pollen meiosis starts just before the ear emerges and is spread over a few days. Irregularity in meiosis results in a reduction in the level of seeds set, but a regular meiosis does not necessarily result in a high level of seed set (Doussinault *et al.* 1988). Grain number per ear can be limited by pollen sterility induced by climatic stresses at meiosis, such as water deficit (Saini and Aspinal, 1981) heat stress (Siani and Aspinal, 1982), low radiation (Demotes-Mainard *et al.* 1995) or low temperatures (Kim *et al.*, 1985; cited in Demotes-Mainard *et al.* 1995). Water stress at this time can reduce male sterility (Binham, 1966; Saini and Aspinall, 1981). Heat stress can affect both male and female sterility (Saini *et al.*, 1983). Shade during stem elongation reduces the number of grains per ear and a combination of low irradiance and low temperature during meiosis further reduces grain number as a result of pollen sterility (Demotes-Mainard *et al.*, 1996).

Variety pedigrees are also implicated in susceptibility to infertility. Tables 8 and 9 indicate that many varieties with low fertility have common parents. Most striking are the two lines 94.11 and 94.08 which are both very closely related to Moulin. These lines showed very severe yield losses in the Aberdeen site and low levels of fertility. Another line implicated is Talon which showed reduced levels of ear fertility in 1995 following late frosts. This is present in the parentage of Pentium which was the lowest yielding NL2 variety at the Aberdeen site.

The advantage of the UK testing system is that candidate varieties are exposed to a range of environmental conditions. Even relatively small environmental changes may produce effects on yield in sensitive varieties. This testing regime is thus likely to expose varieties which would be deemed to be 'at risk' from reduced ear fertility levels. However if varieties are tested in a sequence of years when key environmental stresses are absent varieties with a sensitivity to reduced ear fertility may not be noticed with consequential risk to growers.

Genetic control of fertility is likely to be linked to the development of other plant characters such as timing of ear development and modification of plant height. Breeding programmes designed to improve yield and disease resistance may also introduce genetic material that influences fertility. The genetic control of flowering time is determined by a series of photoperiod sensitive, vernalisation sensitive and earliness genes that are also directly associated with spikelet number and fertility (Worland, 1996). The Norin 10 semi-dwarfing genes, present in all UK semi-dwarf wheat varieties, increase yield and spikelet fertility (Gale and Youssefian, 1985). However, if varieties carrying the dwarfing genes are exposed to adverse climatic conditions or stress (e.g. high temperature) in the period between flag leaf and ear emergence then both fertility and yield may be reduced (Worland *et al.* 1989).

Conclusions and recommendations

A) This study has demonstrated a significant relationship between yield and fertility across varieties grown at the same location. Fertilities below 60-65% are likely to result in a significant loss of yield. A definition of a 'normal' or typical fertility level has a range between 65-90% and is dependent on variety and site. The definition of 'normal' could be made more precise by assessing yield and sterility at a wider range of sites in the UK.

B) Some varieties are more susceptible to floret sterility than others, and some varieties appear to compensate better than others for a loss of grain number as a result of floret sterility. Varieties are particularly vulnerable to yield loss when sterility has resulted in less than 2 grains per spikelet on average.

C) The proportion of sterile grain sites counted at the base of the ear was approximately 0.25 regardless of overall fertility level. Hence, counts of grains and sterile sites at the base should provide a good indication of ear fertility.

D) Exposure to extremes of weather conditions at growth stages between terminal spikelet and anthesis have been implicated in the loss of fertility. Further work needs to be undertaken to establish how conditions such as low temperature (degree and duration), low irradiance and nutrient stress affect floret development and especially meiosis.

E) We are now in position to test hypotheses founded on 'effects of weather conditions at critical stages of floret development on fertility in susceptible and less susceptible varieties'. Such work should include controlled environment studies backed up with more comprehensive studies of geographical/climatic factors in the field. Measurements of fertility and components of yield (e.g. ears per unit area and mean grain weight) would enable:

(i) A more precise definition of a 'normal' level of fertility.

(ii) An improved model for describing the relationship between fertility and yield.

(iii) A means to quantify the effect of fertility *per se* on varietal yield differences within and between locations.

(iv) Development of procedures (e.g. defined conditions and varietal traits) to examine interactions between environmental and genotypic controls of fertility.

F) Experimentation along the lines of that indicated in G) would enable the following questions to be addressed:

(i) Can inherent differences in fertility between varieties across a number of locations be quantified?

(ii) Are differences in fertility between current NL or RL varieties greater than expected?

(iii) Are low mean yields in UK variety trials a consequence of reduced levels of fertility across most or all sites?

(iv) Would some varieties perform better nationally if they had a higher level of fertility?

(v) To what extent do other components of yield, such as ears per unit area and mean grain weight, compensate for a loss of fertility?

(vi) To what extent is a crop's ability to compensate for reduced fertility influenced by genotype and management practice?

G) The development of environmental tests and, in the longer term, genetic tests should enable growers to make a more informed decisions about the choice of variety for local conditions and assist breeders in the development of less vulnerable varieties. This would prevent high risk varieties from entering the Recommended List. A more detailed examination of variety pedigrees and the genetic make-up of both susceptible and less susceptible varieties or breeding lines could identify genes that control or modify the expression of fertility.

H) The results of this study are likely to influence breeding programmes as breeders discard material that might expose them and growers to vulnerable varieties. Thus, the main benefit for the industry is avoiding what could be very costly decisions for growers and breeders.

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